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Miocene Leptomerycidae (Artiodactyla, Ruminantia) and Their Relationships

BERYL E. TAYLOR[1] AND S. DAVID WEBB[2]

ABSTRACT

Leptomerycidae, previously thought to have survived only into the Arikareean, are here recognized from the medial Miocene (late Hemingfordian into Valentinian) deposits of New Mexico, Texas, and Nebraska. These late-surviving Leptomerycidae belong to the species *Pseudoparablastomeryx scotti* and *P. francescita*, previously assigned to the Blastomerycinae. Likewise, *Pronodens silberlingi* from Arikareean deposits in Montana and possibly South Dakota is transferred to the Leptomerycidae from *incertae sedis* in the Cervidae.

The relationships between these late Leptomerycidae and contemporaneous Blastomerycinae are shown to be remote despite several parallel features in common. Separation of the family Leptomerycidae from the family Hypertragulidae is advocated.

INTRODUCTION

The small Oligocene traguloid, *Leptomeryx evansi*, is probably the most abundant ungulate in the vast collections of fossil vertebrates from the White River Badlands of South Dakota (Clark and Guensberg, 1970, p. 412). *Leptomeryx* was thought to have become extinct by the end of the Oligocene until Matthew (1926, p. 4) recognized the survival of one species into the early Miocene, in his "Lower Rosebud" beds and "Lower Harrison" deposits. Later Cook (1934, p. 155) described a new species of *Leptomeryx* (*L. agatensis*) from the "Lower Harrison formation" of Nebraska. Such early Miocene occurrences have been confirmed more recently by Macdonald's (1963, 1970) studies in the Wounded Knee area in South Dakota.

The purpose of the present paper is to provide additional evidence to support the Leptomerycidae as a distinct family and to recognize the survival of two leptomerycid genera into much younger stages of the Miocene. Neither of the genera here recognized as Leptomerycinae are new taxa. Rather, they are transferred from other assignments within the Cervidae, in one case from the more progressive immigrant subfamily Blastomerycinae[1] (Frick, 1937), and in

[1] Blastomerycinae Frick, 1937, New Rank (=Blastomerycini) [including Longirostromerycinae Frick, 1937 and Parablastomerycinae Frick, 1937.] Frick's (1937) taxonomic arrangement recognized "Divisions" with names ending in "ini" as an intermediate rank between family and subfamily. With the exception of *Pseudoparablastomeryx*, we recognize all taxa included in Frick's revision of the "Blastomerycini" as belonging to the Blastomerycinae.

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the other from an uncertain status within the Cervidae (Koerner, 1940; Simpson, 1945). This new evidence raises the question of how these later leptomerycines survived the period when great herds of blastomerycines and dromomerycines spread so abundantly across North America, but it does not provide a clear answer. Evidently their Oligocene level of abundance had declined severely during the Miocene. Possibly they survived as relicts in forested habitats.

ACKNOWLEDGMENTS

Our thanks to Drs. Malcolm C. McKenna and Richard H. Tedford for reading the manuscript and for giving helpful suggestions. We are grateful to Dr. John H. Ostrom of the Peabody Museum, Yale University for lending us the type of *Pronodens silberlingi.* The illustrations were prepared by Mr. Raymond J. Gooris, and the manuscript was typed by Miss Janice Ebenstein.

ABBREVIATIONS

Institutional:

AMNH, Department of Vertebrate Paleontology, the American Museum of Natural History

F:AM, Frick American Mammals, Department of Vertebrate Paleontology, the American Museum of Natural History

FBAM, Frick Barbour, American Mammals, Department of Vertebrate Paleontology, the American Museum of Natural History

YPM, Peabody Museum, Yale University

Used in Figures:

PS, postsymphysis

Used in Measurements and Statistics:

N, sample size

OR, observed range

$\bar{X}$, mean

S, standard deviation

V, coefficient of variation

SYSTEMATICS

ORDER ARTIODACTYLA OWEN, 1848

SUBORDER RUMINANTIA SCOPOLI, 1777

INFRAORDER TRAGULINA FLOWER, 1883

FAMILY LEPTOMERYCIDAE ZITTEL, 1893

In retaining the Leptomerycidae as a family we follow Gazin's (1955) cogent argument. As he noted (pp. 12, 43, and 55) "striking dissimilarities in details of dentition" indicate separate origins for the Hypertragulidae and the Leptomerycidae, in which case "retaining these in the same family . . . is untenable." Moreover, we find that fundamental cranial and postcranial differences also support Gazin's conclusion (see Relationships, p. 19). Subsequent transfer of various late Eocene genera from Gazin's Leptomerycidae to become early members of the Protoceratidae, as advocated by Wilson (1974, p. 30) and partly anticipated by Romer (1966, p. 283), does not affect this, for such a reduction in generic content of the Leptomerycidae does not alter its phylogenetic relationship to the Hypertragulidae. It is ironic that Scott's (1899, p. 15) original usage of "Leptomerycidae" included the hypertragulids at subfamily level. Another curiosity about the name "Leptomerycidae" is Scott's (1945, p. 229) attribution of the name to Osborn. In the present paper we deal only with the subfamily Leptomerycinae. The possibility that the subfamily Archaeomerycinae should be included in the Leptomerycidae will be considered in a separate contribution.

SUBFAMILY LEPTOMERYCINAE ZITTEL, 1893

PRONODENS KOERNER, 1940

Figure 1C-E

Pronodens Koerner, 1940, p. 842, pl. 2, figs. 3.

Leptomeryx obliquidens Lull, 1922, p. 115: specimen referred by Matthew, 1926, p. 4.

Type Species. Pronodens silberlingi Koerner, 1940.

Included Species. Type species only.

Type. YPM 13952, left incomplete mandibular ramus with I_1-I_2, I_3-C (alveoli), and P_2-M_3 (broken) recorded from the Fort Logan Formation (Arikareean) Section 4, R. 10 N., T. 5 E., Meagher County, Montana.

Known Distribution. Arikareean of Montana and South Dakota.

Tentatively Referred. AMNH 13824, right partial maxilla with P^2-M^2, listed by Matthew, 1926, from "Lower Rosebud beds near No Flesh Creek, Pine Ridge Indian Reservation, S. Dakota."

Revised Diagnosis. Differs from *Leptomeryx* in loss of P_1; shorter diastema between C and P_2; posterior extension of symphysis to a point below anterior root of P_2; relatively smaller premolars; a reduction in size of paraconid on premolars; and more posterior position of mental foramen below anterior border of P_2.

Differs from *Pseudoparablastomeryx* in its larger size; diastema between C and P_2 less elongate, more robust and dorsoventrally deeper; mental foramen situated less anteriorly and beneath anterior border of P_2; and symphysis extended more posteriorly with posterior border beneath anterior root of P_2.

Discussion. Koerner (1940) initially described *Pronodens* and placed it in the Cervidae. The type of *P. silberlingi* is an incomplete mandibular ramus and the only specimen known to him. In the generic diagnosis Koerner listed the following characters: strongly procumbent, tusklike incisors, the unusually short diastema between the canine and P_2, and the posterior position of the mental foramen along with the posterior extension of the posterior border of the mandibular symphysis, both to a point below the anterior part of P_2. Koerner (1940, p. 844) stated, "In spite of the unusual character of the incisors, *Pronodens* is undoubtedly one of the pecorans. The general features of the grinding teeth and the absence of P_1, seem to indicate that its closest affinities are with the Cervidae."

Of course the most striking feature of the type mandibular ramus of *P. silberlingi* is the strongly procumbent tusklike incisors. The procumbent incisors can now be nearly duplicated (fig. 1B) in position, size, and wear pattern with those of *Leptomeryx* (cf. *Leptomeryx mammifer* Cope) mandibular ramus (F:AM 95493) from the Chadronian of Montana. Both I_3 and the canine, which are represented by alveoli in the type of *P. silberlingi*, are present in the *Leptomeryx* jaw. I_3 in *Leptomeryx* is slightly smaller than I_2 and the canine is incisiform and adjacent to I_3 with the crown approximating that of I_3 in size but with a more robust root. The alveoli for I_3 and the C in the type of *P. silberlingi* correspond to those of the same teeth in *Leptomeryx* with the alveolus for the canine slightly larger than that of I_3.

Many characters distinguishing *Pronodens* from *Leptomeryx* are associated with the shortening of the anterior part of the mandibular ramus. These include the abbreviation of the post canine-P_2 diastema and the posterior shifting of the symphysis and mental foramen to a point below the anterior part of P_2. The loss of P_1 may also be associated with the foreshortening of the diastema. Furthermore, we have observed that P_2-P_4 are less elongate and relatively smaller than in *Leptomeryx* with a proportionally shorter paraconid accounting, at least, for a part of this reduction in size. A prominent and labially projecting hypoconid is present on P_3 and P_4 of both the type of *Pronodens silberlingi* and the above *Leptomeryx* (cf. *L. mammifer*) mandibular ramus (F:AM 95493). Although the worn molars of the type of *P. silberlingi* closely resemble those of *Leptomeryx*, extreme wear precludes any detailed comparison of morphological features.

Matthew (1926, p. 4) referred an upper jaw (AMNH 13824) from the Lower Rosebud beds to *Leptomeryx obliquidens* Lull and observed that the jaw is slightly smaller than Lull's type. Regarding AMNH 13824 Frick (1937, p. 624) stated, "there may be considerable doubt as to the allocation of the partial cheek-tooth series from the middle Tertiary deposits between the Leptomerycini and the Blastomerycini." Frick noted that the lingual midroot and protocone of P^3 and P^4 are as prominently developed as in *Pseudoblastomeryx falkenbachi* and stated, "Should the specimen be of Blastomerycini, it may belong to *Problastomeryx primus* of the same beds . . . [and] (if of the Leptomerycini, it would seem to represent a species lying near to *L. transmontanus* Douglas of the pre-Rosebud of Montana)." A comparison of the premolars of the above maxilla (AMNH 13824) with the worn teeth of the type of *Problastomeryx primus* shows that the protocone of P^3 is more detached and supported by a strong separate root. Moreover, P^3 differs from that of the type of *Problastomeryx primus* in the absence of strong anterolingual and posterolingual cingula connecting with the protocone to enclose a well-developed fossette. The paracone is situated more posteriorly than in *Problastomeryx* and almost directly opposite the protocone as in *Leptomeryx*. Unfortunately P^2 is absent in the type of *Problastomeryx primus*, but a comparison of this premolar with that of a skull (F:AM 31531) of

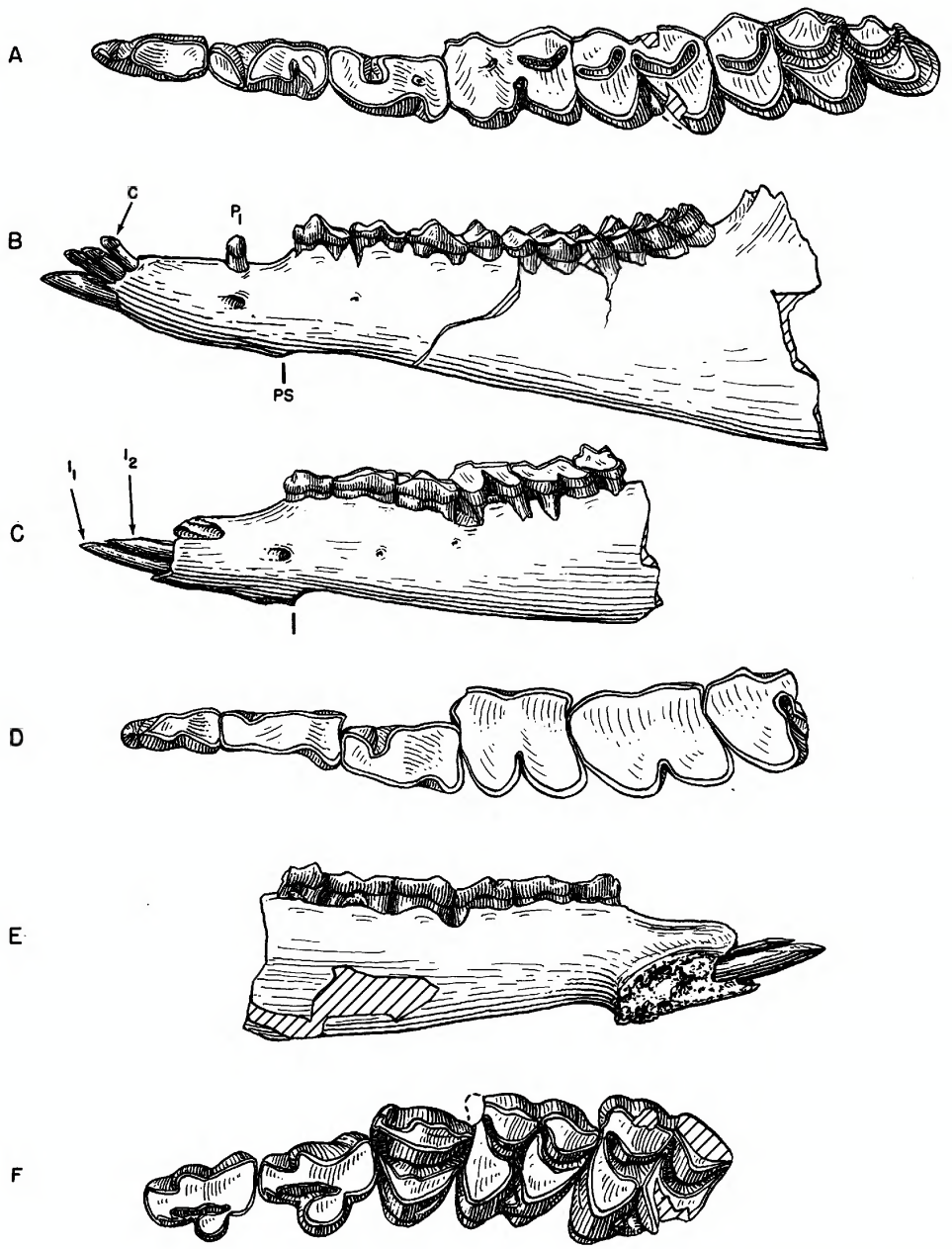

FIG. 1. A, B. *Leptomeryx mammifer*, referred right ramus, F:AM 95493, from the White River Formation, Natrona Co., Wyoming; A. Occlusal view, reversed. X2. B. Lateral view, reversed. X1. C-F. *Pronodens silberlingi.* C-E. Type ramus, YPM 13952, from the Fort Logan Formation, Montana; C. Lateral view. X1. D. Occlusal view. X2. E. Lingual view. X1. F. Referred maxilla, AMNH 13824, from the "Lower Rosebud Beds," South Dakota, occlusal view, reversed. X2.

Pseudoblastomeryx falkenbachi shows that the above morphological difference between P^3s also applies to P^2s of these taxa.

Hence, we agree with Matthew that the upper jaw is an Arikareean leptomerycid. Matthew apparently referred this maxilla to *L. obliquidens*

with some reservation and pointed out that the molars "do not show the markedly oblique set of crescents noted in his type." A comparison of this much larger maxilla with the type of *Leptomeryx agatensis* (Cook) from the Harrison Formation in Nebraska shows no significant morphological difference except size. The dentition of the upper jaw (AMNH 13824) has the characteristic features of *Leptomeryx*, and the P^2-M^2 length (38.5 mm.) is almost identical to that of the corresponding teeth of the type lower jaw (YPM 13952) of *Pronodens silberlingi.* Because the diagnostic characters of *Pronodens* are based on the morphological features of the anterior part of the ramus and not on the cheek teeth that resemble those of *Leptomeryx*, the only remaining criterion is size, and on this basis we tentatively refer the South Dakota upper jaw (AMNH 13824) to *Pronodens silberlingi.*

PSEUDOPARABLASTOMERYX FRICK, NEW RANK

Parablastomeryx (*Pseudoparablastomeryx*) Frick, 1937, p. 244.

Type Species. Pseudoparablastomeryx scotti Frick, 1937.

Included Species. Type and *Pseudoparablastomeryx francescita* (Frick, 1937).

Known Distribution. Late Hemingfordian to Valentinian of Nebraska, Texas, and New Mexico.

Revised Diagnosis. Differing from *Leptomeryx* in having the skull more brachycephalic; P^2 and P^3 shorter relative to the length of the molars with broader stronger anterolingual and posterolingual cingula; symphysis less elongate and shallower with posterior border of symphysis not reaching a point below P_2 and terminating even more anteriorly than in *Leptomeryx*; P_1 lost; P_2-P_4 smaller relative to size of molars; molars narrower and more compressed with a well-developed buttress on protoconid and a stronger median pillar on crown between the protoconid and hypoconid; M_3 entostylid greatly reduced; metacarpals II and V greatly reduced, III and IV fused to form a cannon bone; and a stronger and more anteriorly extended keel on distal trochlea of metapodials.

Differing from *Pronodens* in its smaller size; diastema between C and P_2 more elongate, less robust and shallower; mental foramen situated more anteriorly about midway between C and P_2; and symphysis shorter with posterior border of symphysis forward of P_2.

Discussion. Frick (1937, p. 244) originally described *Pseudoparablastomeryx* as a subgenus of *Parablastomeryx.* Some doubt as to the status of *Pseudoparablastomeryx* was indicated by Frick's (1937, p. 219) description of the type jaw as "A diminutive mandibular ramus with large, stubby-proportioned premolars and an abbreviation of the diastema exceeding that of *Parablastomeryx*, is tentatively placed under the latter as a subgenus. . . ." Additional material shows that *Pseudoparablastomeryx* is clearly different from all members of the Blastomerycinae. The diagnostic characters of *Pronodens* and, in part, those of *Pseudoparablastomeryx* are based more on the morphological characters of the anterior part of the mandibular ramus, the incisors, and the canine than on the morphology of the cheek teeth. The last in both the Blastomerycinae and the Leptomerycinae are fundamentally similar.

The derived morphological characters that distinguish *Pseudoparablastomeryx* from the Blastomerycinae are held in common with the Leptomerycinae. These characters are (1) small upper canine, (2) elongate symphysis, (3) procumbent incisors including a large tusklike I_1 with an extremely tall crown and a long root, and (4) small procumbent lower canine. Because of the above features in common with the Leptomerycinae, *Pseudoparablastomeryx* is placed in this subfamily.

Several features distinguish *Pseudoparablastomeryx* from *Leptomeryx.* The skull of *Pseudoparablastomeryx* is more brachycephalic. Outstanding dental characters that distinguish *Pseudoparablastomeryx* from *Leptomeryx* are the loss of P_1, the relatively smaller premolars, the more compressed lower molars with a well-developed anterobuccal buttress. Diagnostic features of the metapodials include a strong distal keel, extreme reduction in size of metacarpals II and V, and the fusion of metacarpals III and IV. Because of these differences, we have elevated *Pseudoparablastomeryx* to generic rank.

Pseudoparablastomeryx scotti
Frick, 1937
Figures 2B-C, 3A-D, 4, 5B, E-H, 6.
Tables 1, 2

Parablastomeryx (Pseudoparablastomeryx) scotti Frick, 1937, p. 244, figs. 22A, 23B.

Type. FBAM 33763, right mandibular ramus with symphysis and P_2 (root)-M_3(broken) from Observation Quarry (early Barstovian) Dawes County, Nebraska. Figured by Frick, 1937, fig. 22A; present report, figs. 4A, B.

Known Distribution. Late Hemingfordian of Sioux County, Nebraska, early Barstovian of Sioux and Dawes counties, Nebraska, and San Jacinto County, Texas.

Referred Material (from the type location). F:AM 95478, right partial maxilla with M^2-M^3; F:AM 95479, right partial maxilla with M^1-M^2 (broken); F:AM 95481, seven isolated upper molars; F:AM 95482, five isolated upper molars; F:AM 33767, right partial maxilla with P^3-M^3; F:AM 95476, left partial maxilla with P^4-M^3; F:AM 53391, left maxilla with P^2-M^3 (molars broken); F:AM 53392, left maxilla with M^3; F:AM 95484, right partial ramus with M_1-M_3; F:AM 95486, right ramal fragment with M_1-M_2; F:AM 95487, right ramal fragment with M_3; F:AM 95488, right ramal fragment with M_1; F:AM 53382, right partial ramus with M_1 (broken)-M_3; F:AM 53383, right partial ramus with M_2-M_3; F:AM 53384, right partial ramus with M_1-M_2; F:AM 53385, right partial ramus with M_3; F:AM 53386B, three isolated M_3s; F:AM 33768, right partial ramus with symphysis, P_2 (alveolus)-M_2 (broken); F:AM 33769, right partial ramus with M_1-M_3; F:AM 95483, left partial ramus with M_1-M_3; F:AM 53387, left partial ramus with M_1-M_3; F:AM 53388, left partial ramus with M_1-M_2; F:AM 53389, left partial ramus with P_4-M_1 (broken); F:AM 53390, left partial ramus with diastema and P_2-P_3; F:AM 34026, left partial ramus with P_4 (root)-M_3; F:AM 95477, right immature partial maxilla with dP^4-M^3; F:AM 95480, right immature partial maxilla with dP^4-M^1; F:AM 53394, left immature maxilla with dP^2-M^2; F:AM 95485, right partial immature ramus with dP_4-M_2; F:AM 53393, left partial ramus with dP_4-M_1; F:AM 53393-A, left partial ramus with M_1-M_2 (erupting); FBAM 33766-A, left distal end of humerus (Frick, 1937, fig. 23B; present paper, fig. 6A); FBAM 34027, right radius (Frick, 1937, fig. 23B; present paper, fig. 6B-D); FBAM 33766, right proximal part of radius; FBAM 33765, right metacarpus (Frick, 1937, fig. 23B; present paper, fig. 6E-F); FBAM 33764, left metatarsus (Frick, 1937, fig. 23B; present paper, fig. 6G-H); F:AM 95491, left metatarsus (fig. 6I); and FBAM 34027-A, right metatarsus (Frick, 1937, fig. 23B).

From Hilltop Quarry, Sheep Creek beds (late Hemingfordian) Sioux County,[1] Nebraska: F:AM 53403, left partial ramus with M_3; and F:AM 53404, left immature partial ramus with dP_3-M_3 (erupting and broken).

From the Lower Snake Creek beds (early Barstovian) Sioux County, Nebraska: F:AM 53395, right ramus with symphysis, I_1 (broken) and P_2-M_3 from Jenkins Quarry; F:AM 53396, right ramus with symphysis and I_1-C (alveoli) and P_2 (root)-M_3 from East Jenkins Quarry; F:AM 53397, left partial maxilla with P^2-M^3 (M^1 broken), M^2 root) from East Jenkins Quarry; F:AM 53398, left partial ramus with P_3 (alveolus)-M_3(broken) from West Surface Quarry; F:AM 53399, left fragmentary ramus with P_2-P_4 (broken) from New Surface Quarry; F:AM 53400, right immature partial ramus with broken diastema and dP_2-M_3 (germ fragment) from New Surface Quarry; F:AM 53401, right partial ramus with M_1-M_3 (broken) from Humbug Quarry; F:AM 53402, left partial ramus with M_2-M_3 from Quarry 2; AMNH 14131, right metatarsus (Matthew and Cook, 1909, fig. 25; Frick, 1937, fig. 25A) Snake Creek beds; and F:AM 95492, right metatarsus with distal end broken, East Sand Quarry.

From Trinity River Pit 1, 7 miles northeast of Cold Spring (latitude 30° 40′ 15″ N, longitude 95° 03′ 10″ W), San Jacinto County, Texas. The quarry is on the south bank of the Trinity River, about 1000 feet downstream from the mouth of Prayer Creek, directly below a high point or bluff known locally as Pine Island Hill. Trinity River Pit 1 is in the upper part of the Fleming Formation and lithologically 225 to 300 feet below the

[1] The stratigraphy of the late Cenozoic deposits in Sioux County, Nebraska is being prepared for publication by M. F. Skinner, S. M. Skinner, and R. J. Gooris.

lithic zone from which the published Cold Spring Fauna of Wilson (1956) was derived, according to the unpublished stratigraphic data of M. F. Skinner on file in the American Museum of Natural History: F:AM 95490, an almost complete but somewhat crushed skull with premaxilla missing, C (alveolus broken) and P^2-M^3; and F:AM 95489, right partial immature ramus with dP_2-M_3 (germ).

Revised Diagnosis. P. scotti differs from *P. francescita* in molars averaging larger (tables 2, 3); P_3 and P_4 smaller relative to the size of molars, and molars less compressed, more robust, and lower crowned.

Description. Skull: The only skull of *Pseudoparablastomeryx* presently known is from the Trinity River Pit 1, in Texas (F:AM 95490). Because the upper dentition is closely comparable to upper dentitions of *P. scotti* from Observation Quarry in Nebraska, we refer the skull to the species. The skull is nearly complete, lacking only the premaxillary region, but it was crushed from the top downward, the resulting distortion obscuring some details, especially in the basicranial and orbitotemporal regions.

This skull is far more brachycephalic than skulls of *Leptomeryx evansi.* The proportional differences exceed any that can be attributed to the imperfections of preservation, although that may contribute. The minimum postorbital breadth, measured across the frontals, is 28 mm. in the skull of *Pseudoparablastomeryx scotti*, whereas in two undistorted specimens of *Leptomeryx evansi* with similar tooth row length, the postorbital breadth is less than 24 mm. On the other hand, the axial distance from between the postorbital constrictions to the nuchal eminence is just under 36 mm., whereas in the two skulls of *L. evansi* this distance is more than 40 mm. Other measurements that would reflect the proportions of the braincase are not to be trusted, owing to evident distortions of the bones. If the ratio of postorbital width to braincase length is taken as an index of brachycephaly, then the cranium of *P. scotti* has an index of about 0.8, whereas the two crania of *L. evansi* have index values of less than 0.6.

The other distinctive features of the braincase are presumably correlated with the more brachycephalic proportions of the cranium of *Pseudoparablastomeryx.* First, the sagittal crest is short and low. It measures only 12 mm. long, whereas in each of the two skulls of *L. evansi* the sagittal crest exceeds 20 mm. in length. Second, the nuchal eminence and occipital crests do not markedly overhang the occipital surface, nor is the supraoccipital region deeply pocketed for insertion of nuchal ligaments as in crania of *L. evansi.* Both of these features seem to reflect the general shortening of the posterior part of the cranial vault in *P. scotti.*

The facial region is also shorter in the cranium of *P. scotti* than in skulls of *L. evansi.* The distance from the anterior wall of the orbit to the posterior edge of the canine alveolus is just under 33 mm., whereas in comparable skulls of *L. evansi* that distance is more than 42 mm. Abbreviation of the rostrum is further indicated by the short postcanine diastema in *P. scotti*, described below. Because the premolars are also reduced, the short diastema of *Pseudoparablastomeryx* is all the more remarkable. Thus the facial region and the cranium both reflect the brachycephalic proportions of the skull of *P. scotti.*

Other proportional features of the skull may exist, but the possibility of serious distortions cannot be eliminated. For example, the last upper molar lies beneath the postorbital bar in *P. scotti*, whereas in mature individuals of *L. evansi* the last molar lies below the middle of the orbit. Also, the pterygoid and orbitotemporal region is strongly compressed, but much, if not all, of this effect results from crushing. The arrangement of the masseter muscles differs considerably also. In *P. scotti* the masseteric crests project farther laterally than in *L. evansi*, and the anterior margin of the masseter reaches only a midorbital rather than an anterorbital position.

In most other respects the skull of *P. scotti* resembles that of *L. evansi.* Nonetheless, the following more detailed notes may be of interest. The anterior palatine foramen opens opposite M^1, whereas in mature specimens of *L. evansi* it usually emerges opposite the middle of M^2. The infraorbital foramen lies above the anterior root of P^2, whereas in *L. evansi* it opens above the posterior root of that tooth. This presumably results from the premolars shortening and retracting relative to the position of the foramen.

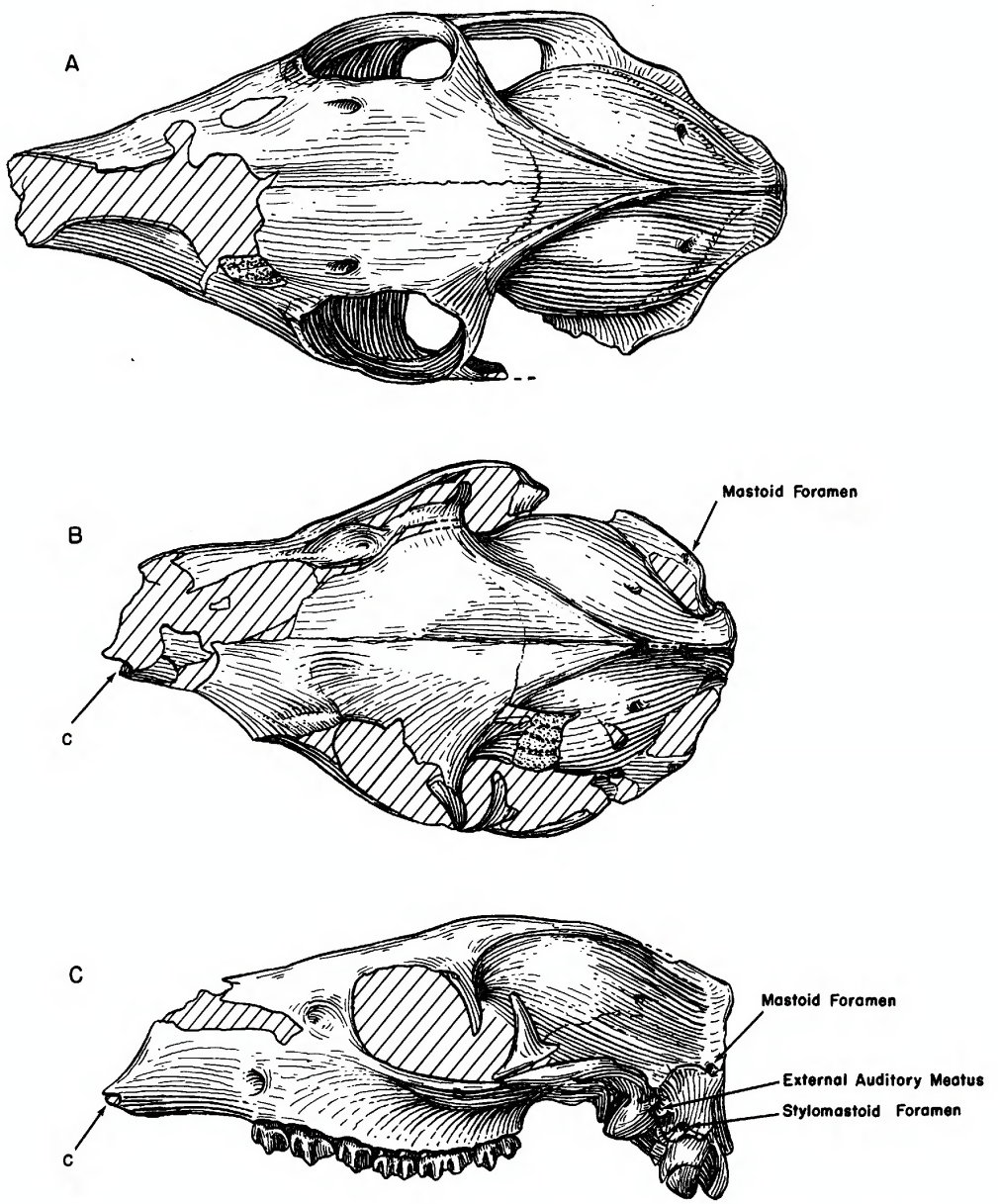

FIG. 2. A. *Leptomeryx evansi*, skull, AMNH 39123, from the Scenic Member of the Brule Formation, South Dakota; dorsal view. B, C. *Pseudoparablastomeryx scotti*, partial skull, F:AM 95490, from the upper part of the Fleming Formation, San Jacinto Co., Texas; B. Dorsal view. C. Lateral view. All × 1.

Even though the lacrimal region is badly crushed, the shape of the lacrimal bone in the position of the lacrimal vacuity can be seen to agree generally with those in *L. evansi.* The nasal bones are missing. The interorbital width between the frontals is probably greater than in *L. evansi.* The supraorbital foramina are very large and, at least, on the right side, they lead

anteriorly into large canals, even more conspicuous than in crania of *L. evansi.* The large parietal foramina noted by Scott (1940, p. 544) in *L. evansi* also occur in *P. scotti*, but here they lie 12.5 mm. from the midline, whereas even in larger specimens of *L. evansi* they lie only 8 or 9 mm. to the side. The postorbital bar and zygomatic arch are badly broken, yet they appear to have had about the same arrangement as in *L. evansi.*

The left half of the basicranial region retains the glenoid fossa, many parts of the ear region, and the occipital condyle. On the badly shattered right side we have prepared the ventral aspect of the petrosal bone. In *P. scotti* the glenoid fossa is shallower than in *L. evansi*, and the postglenoid process is reduced especially toward the lateral margin. The anteromedial end of the bulla appears less inflated than in *L. evansi*, and the channel for the stylohyoid reaches almost to the anteromedial part of the bulla, whereas in *L. evansi* it does not enter the middle of the bulla. The posterolateral portion of the bulla, including the auditory meatus, is badly fractured. The base of the paraoccipital process has the same size and position as in *L. evansi*, and the stylomastoid foramen is similarly located. The general outline of the mastoid exposure resembles that in *L. evansi*, but the mastoid crest, well developed in that species, is only weakly developed in *P. scotti.* Furthermore, the mastoid foramen is much smaller than in *L. evansi* and lies above rather than below the mastoid crest. The occipital condyle seems slightly shallower in the posterior view than in *L. evansi.* The ventral aspect of the right petrosal of *P. scotti* agrees in all of its details with that of *L. evansi.*

Upper Dentition. In most respects the upper dentition of *P. scotti* closely resembles that of *L. evansi*; important differences are found only in the anterior premolars. The best representation of the upper dentition is provided by a skull from Trinity River Pit 1 in Texas, F:AM 45490, although several maxillary fragments from Observation Quarry in Nebraska help confirm the features of the cheek teeth.

The presence of a small upper canine is indicated by an alveolus about 2 mm. in diameter lying next to the left premaxillary suture. Scott (1940, p. 538) stated that the upper canine of *L. evansi* can have had no function, and that would seem true in this genus as well. If so, this represents a notable example of a vestigial structure being retained through two full epochs. The postcanine diastema is 14.2 mm. long, shorter than in many similar-sized specimens of *L. evansi* but this is attributable to individual variation, as the larger sample of lower jaws shows no such feature.

The anterior premolars, P^2 and P^3, closely resemble each other and are almost identical in length, as in *L. evansi.* As in that species the protocone is stronger on P^3 and consequently that tooth is wider. The protocone on each premolar is midlingual and supported by a small lingual root as in *Leptomeryx.* (Scott's statement that P^2 of *Leptomeryx* had no lingual root is in error, as careful scrutiny of several specimens has shown.) The principal difference from *L. evansi* is the presence of broad strong anterolingual and posterolingual cingula. With wear they enclose a long posterior and a short anterior fossette. In *L. evansi* these cingula are weak on P^3 and sometimes absent on P^2. The posterolingual cingulum of *P. scotti* unites broadly with the protocone; whereas the anterolingual cingulum is separated from it by a deep notch. The broadened posterolingual region of these premolars wears as an extension of the lingually sloped paracone-metacone surface. The parastyle of P^2 and P^3 are higher and narrower in labial view than in *L. evansi.* And P^2 and P^3 are shorter relative to the molars than in *L. evansi.*

P^4 of *P. scotti* differs from that of *L. evansi* in its narrow parastyle and in the presence of weak lingual cingulum.

The upper molars retain the characteristic features of *L. evansi.* The anterior end of the posterior crescent does not join the posterior end of the anterior crescent and only weakly approaches the mesostyle. No accessory folds enter the principal fossettes. The parastyle, mesostyle, and anterior rib are very strong, and the posterior rib is weak. M^2 is the largest molar, and the posterior half of M^3 is reduced. A midlingual pillar occurs on each molar; it is larger on M^2 than on M^1, and is largest and partly twinned on M^3. The enamel surface is finely crenulated on the cheek teeth, and they bear no cement.

No species of *Leptomeryx* presently known

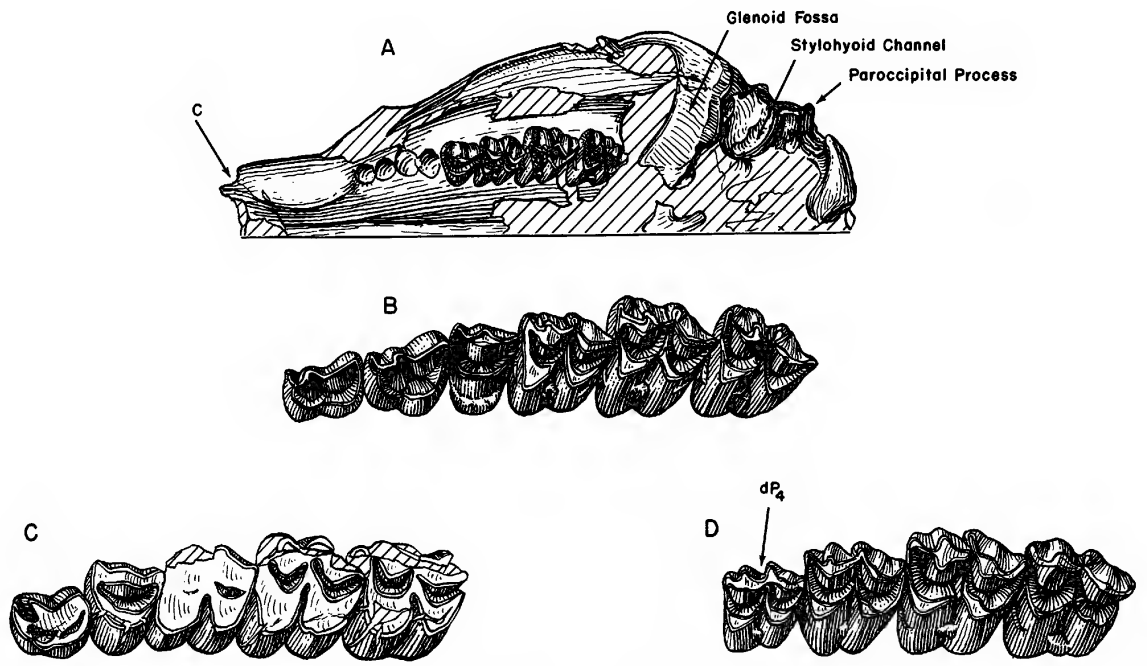

FIG. 3. A-D. *Pseudoparablastomeryx scotti.* A, B. Partial skull, F:AM 95490, from the upper part of the Fleming Formation, San Jacinto Co., Texas; A. Palatal view. X1. B. Right P^2-M^3, occlusal view, reversed. X2. C, D. Upper dentition from Dawes Co., Nebraska; C. FBAM 33767, Occlusal view, reversed. X2. D. F:AM 45471; Occlusal view, reversed. X2.

TABLE 1
Measurements (in Millimeters) and Statistics of the Upper Dentition of *Pseudoparablastomeryx scotti* from Sioux and Dawes Counties, Nebraska and San Jacinto County, Texas

		N	OR	$\bar{X}$	S	V
P^2	Length	3	5.1 - 5.8	5.47	0.351	5.466
	Width	3	3.9 - 4.5	4.17	0.305	7.321
P^3	Length	4	5.0 - 5.6	5.30	0.244	4.603
	Width	4	4.4 - 5.2	4.78	0.330	6.910
P^4	Length	5	4.4 - 4.7	4.54	0.114	2.511
	Width	5	5.6 - 6.8	6.14	0.512	8.338
M^1	Length	6	6.0 - 6.9	6.50	0.384	5.907
	Width	6	6.6 - 7.5	6.95	0.314	4.517
M^2	Length	6	6.8 - 8.0	7.45	0.496	6.657
	Width	6	7.3 - 8.5	8.13	0.432	5.311
M^3	Length	10	6.8 - 7.7	7.21	0.307	4.257
	Width	10	7.3 - 8.0	7.65	0.241	3.150

approach the peculiar shortening and broadening of P^2 and P^3 observed in *P. scotti.* Although *Leptomeryx agatensis* Cook (1934) closely approximates *P. scotti* in size and age (Arikareean), the character of P^3 in the type specimen lacks all the derived features noted above for *P. scotti.*

Mandible. A complete mandibular ramus of *P. scotti* is unknown but most of the mandibular characters are provided by three partial rami (F:AM 33763, 34026, and 53396). The mandible of *P. scotti* is similar in general shape to that of *L. evansi* (AMNH 39123) and is characterized by a short diastema, a slender horizontal ramus, and an anteroposteriorly elongate ascending ramus. The symphysis is short and rather delicate as it narrows anteriorly toward the incisive region. It is shallower and anteroposteriorly shorter than in *L. evansi* and strongly marked by interconnecting depressions and projections for loose articulation with the opposite jaw. Besides its smaller size, the symphysis extends less posteriorly than in *L. evansi* with the posterior border nearly opposite

the mental foramen well anterior to P_2, whereas in *L. evansi*, the posterior border extends to a point beneath the anterior part of P_2. An uninterrupted short diastema extends from the C to P_2; its length approximates that in *L. evansi*. A relatively large mental foramen is present on the lateral side of the diastema about midway between the C and P_2. The horizontal ramus is rather long, slender, and shallow with the inferior border of the ramus slightly concave between the posterior border of the symphysis and P_3 and markedly convex beneath M_2 and M_3. Although the ascending ramus is incomplete and the angle of the mandible is broken in the jaws of *P. scotti*, enough is preserved to indicate a strong resemblance to *L. evansi*. The ascending ramus rises at an approximate right angle to the tooth row. Judging by the two incomplete mandibular rami (F:AM 33763 and 34026), the anteroposterior diameter of the ascending ramus is exceptionally long as in *L. evansi*, and the broken angle of the mandible indicates that it too projects posteriorly to a point behind the condyle as in *L. evansi*. The lateral surface of the ventral part of the incomplete ascending ramus is rather smooth with little indication of a depression for insertion of the masseter muscle. The mesial surface of the ascending ramus, however, is marked by a large depression for the M. pterygoideus medialis. One partial ramus (F:AM 34026) has a broken and eroded condyle and an incomplete coronoid process. The coronoid process is anteroposteriorly long at the base as in *L. evansi*. This elongation is exceptional as Scott (1940, p. 544) commented, "Another exceptional feature [of *Leptomeryx*] is the disproportionate size of the coronoid process, which is several times as large as in *Hypertragulus* and even larger, relatively, than in *Poebrotherium*."

Lower Dentition. The lower dentition of *P. scotti* closely resembles that of *L. evansi*. Two mandibular rami from Sioux County, Nebraska, have most of the incisive region preserved (figs. 4F and H). An incomplete I_1 is present in F:AM 53395 and a break on the lateral side of the second ramus (F:AM 53396) clearly shows the alveoli for I_1-C. Frick (1937, p. 244, fig. 22A) referred a third partial ramus (FBAM 33768) to *P. scotti*, but the absence of the incisive region prevented his recognizing the special resemblance to *Leptomeryx*.

The three lower incisors and the incisiform lower canine of *P. scotti* closely resemble those of *L. evansi* both in their position and their relative sizes. In fact, Scott's (1940, p. 539) description of these teeth in *Leptomeryx* applies almost equally well to those of *Pseudoparablastomeryx*. All four teeth are strongly procumbent in both genera. In *P. scotti*, I_1 is so strongly procumbent that its ventral surface makes an angle of only 11 degrees with the horizontal line drawn along the alveolar margin of the jaw. This indicates a slightly more procumbent I_1 than in the type of *Pronodens silberlingi* which rises at a 15 degree inclination from the alveolar line (Koerner, 1940, p. 843). I_1 is much larger than the other incisors with the dorsoventral diameter (2.8 mm.) nearly three times greater than the diameter of the alveolus for I_2. Although I_1 is broken near the base (fig. 4F) it is apparent that the crown was extremely elongate, and the root extends posteriorly for almost the full length of the symphysis. The mesial surface of I_1 is flattened near the base, and the lateral surface is convex. Judging by their alveoli, I_2 and I_3 are approximately equal in size. The alveolus for the canine is adjacent to that for I_3; the canine was evidently a small, procumbent, incisiform tooth, approximating the size of I_2 and I_3.

Unlike *Leptomeryx*, P_1 is missing in *Pseudoparablastomeryx* and this derived character is shared with *Pronodens*.

The lower premolars of *P. scotti* are smaller relative to the size of the molars than in *L. evansi*. From P_2 to P_4, the premolars become progressively larger and more complex. P_2 is elongate, slender, and relatively smaller than in *L. evansi*. As in *L. evansi*, it consists of three principal cusps, the paraconid, protoconid, and hypoconid. The metaconid is missing as in *L. evansi* but a weak ridge is present on the lingual surface of the protoconid of one P_2 (F:AM 53395). A crest extends posteriorly from the protoconid to the hypoconid with a weak spur leading to the posterolingual border of the talonid but no distinct entoconid is present. A small hypoconulid, however, is present.

P_3 is basically similar but more complex than

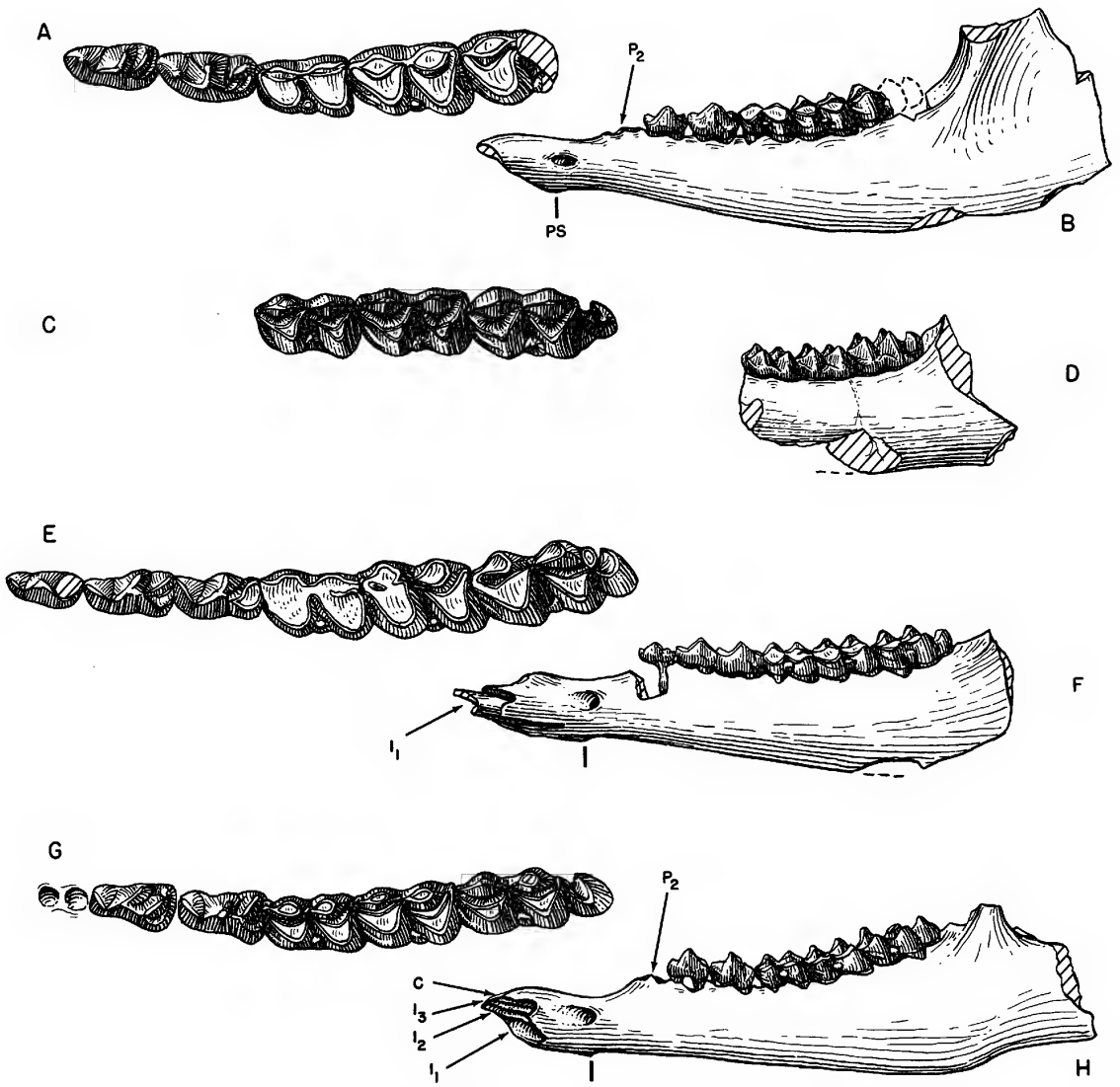

FIG. 4. *Pseudoparablastomeryx scotti*, mandibular rami. A-D, from Dawes Co., Nebraska; A, B, Type. FBAM 33763; A. Occlusal view, reversed. ×2. B. Lateral view, reversed. ×1. C, D. F:AM 95483; C. Occlusal view. ×2. D. Lateral view. ×1. E-H. From Sioux Co., Nebraska; E, F. F:AM 53395; E. Occlusal view, reversed. ×2. F. Lateral view, reversed. ×1. G, H. F:AM 53396; G. Occlusal view, reversed. ×2. H. Lateral view, reversed. ×1.

P_2. In the type (FBAM 37763) P_3 lacks a distinct metaconid, but a strong ridge is present at this point on the lingual surface of the protoconid. The development of the metaconid, however, is considered a variable character because a small, distinct metaconid is present on P_3 of a referred jaw (F:AM 53395). The talonid of P_3 is more complex than that of P_2 with a posterior lingual spur leading to an entoconid which is missing in P_2.

P_4 closely resembles P_3, but all cusps are larger and more distinct. In P_4 the metaconid varies from strong (FBAM 33763) to weak (F:AM 53396). A strong crest extends poster-

TABLE 2
Measurements (in Millimeters) and Statistics of the Lower Dentition of *Pseudoparablastomeryx scotti* from Sioux and Dawes Counties, Nebraska

		N	OR	$\bar{X}$	S	V
P_2	Length	3	4.1 - 4.6	4.43	0.288	6.496
	Width	3	2.0 - 2.4	2.13	0.230	10.782
P_3	Length	7	5.3 - 6.0	5.69	0.285	5.013
	Width	7	2.9 - 3.3	3.06	0.157	4.939
P_4	Length	5	6.0 - 6.7	6.14	0.313	5.097
	Width	5	2.7 - 3.5	3.12	0.327	10.480
M_1	Length	21	5.4 - 7.0	6.42	0.451	7.026
	Width	21	3.2 - 4.7	4.00	0.330	8.241
M_2	Length	19	6.2 - 7.7	7.02	0.452	6.443
	Width	24	4.0 - 5.3	4.46	0.365	8.180
M_3	Length	17	8.4 - 10.4	9.61	0.501	5.212
	Width	17	3.9 - 5.4	4.56	0.415	9.104

iorly from the protoconid to the hypoconid, and a well-developed entoconid is present. Unlike P_3, but as sometimes found in P_4 of *L. evansi*, the entoconid is occasionally connected to the metaconid by a weak crest enclosing a small fossettid.

The lower molars have the basic selenodont pattern and resemble those of *L. evansi* in most respects. They are, however, relatively narrower and more compressed than in that species. The molars are further distinguishable from those of *L. evansi* by a strong buttress at the base of the anterior surface of the protoconid. Although this anterior cingulum-like buttress is occasionally present on molars of *L. evansi*, it is only faintly developed. Furthermore, the median pillar at the base of the crown also averages stronger in *P. scotti* than in *L. evansi*. The crescentic protoconid and hypoconid closely resemble those of *L. evansi* and no diagnostic characters are observed to distinguish the metaconid and entoconid. Except for a greatly reduced entostylid on M_3, all the other stylids are stronger than in *L. evansi*. The parastylid and entostylid are slightly stronger than in the latter, and the metastylid is markedly stronger. Perhaps the most distinguishing morphological character of the lower molars is the great reduction of the entostylid on M_3. In *P. scotti* the size of M_3 entostylid varies from greatly reduced to near missing, whereas in *L. evansi* the entostylid is only about a third smaller than the entoconid and closely resembles the latter. In addition, the hypoconulid of the M_3 in *P. scotti* is comparatively smaller and situated more posteriorly relative to the entostylid than in *L. evansi*. And finally the talonid often takes the shape of a single loop, joining anteriorly with the reduced entostylid, whereas in *L. evansi* the hypoconulid is separated from the large entostylid by a distinct valley.

Deciduous Dentition.[1] The upper deciduous premolars of *Pseudoparablastomeryx scotti*, as indicated by F:AM 53394 from Observation Quarry, have advanced considerably over those of *Leptomeryx evansi*. The major differences all stem from a general tendency for the anterior milk teeth to broaden in *P. scotti*.

dP^2 measures 5.1 mm. long and 3.6 mm. wide and has two roots. The labial wall consists of three cusps of which the central is the highest. The lingual side of the tooth consists of two very strong, very wide cingula each enclosing a shallow fossette; the smaller anterior cingulum joins the larger posterior cingulum on the lingual slope of the central cusp. The larger posterior fossette receives heavy oblique wear from dP_2. In *Leptomeryx evansi*, by contrast, dP^2 has only a faint lingual cingulum, and the wear indicates nearly vertical shearing on the labial cusps. [Scott (1940) did not mention dP^2 or dP_2 in his description of the deciduous dentition of *Leptomeryx*.]

dP^3 is a robust three-rooted tooth, 6.5 mm. long by 5.1 mm. wide. The overall plan of this tooth differs little from that of *Leptomeryx evansi*, which as Scott stated, "has three external cusps in line . . . [and] a posterointernal cusp of crescentic shape." Nonetheless the character of the tooth is dramatically altered because the cusps are all much more robust. The anterior features have an especially different character, for the anterolabial cusp is thick, whereas in *L. evansi* it is as Scott said, "very long, compressed and trenchant." Likewise in *P. scotti* the thick

[1] The cusp terminology used here to describe the deciduous dentition follows that of Loring and Wood, 1969.

anterolingual cingulum joins this cusp to form a shallow fossette, whereas the homologous feature in *L. evansi* is "a faintly marked ridge." The posterior features of dP^3, notably the mesostyle and the posterior crescent, are also much heavier and wider than in *Leptomeryx evansi.* In short, this tooth has assumed a nearly molariform grinding function in *P. scotti*, whereas in *L. evansi* it was in a transitional stage with an emphasis still on shearing.

dP^4 of *P. scotti* is fully molariform and differs from that of *L. evansi* only in being somewhat higher crowned and more robust. The tooth is 6.2 mm. long and 6.1 mm. wide. As Scott noted, the midlingual pillar is more weakly developed than in the molars. The other cusps, however, are almost perfect models, except for their diminished size, of the corresponding molar cusps.

The deciduous lower teeth are best seen in an immature ramus (F:AM 95489) with dP_2-M_3

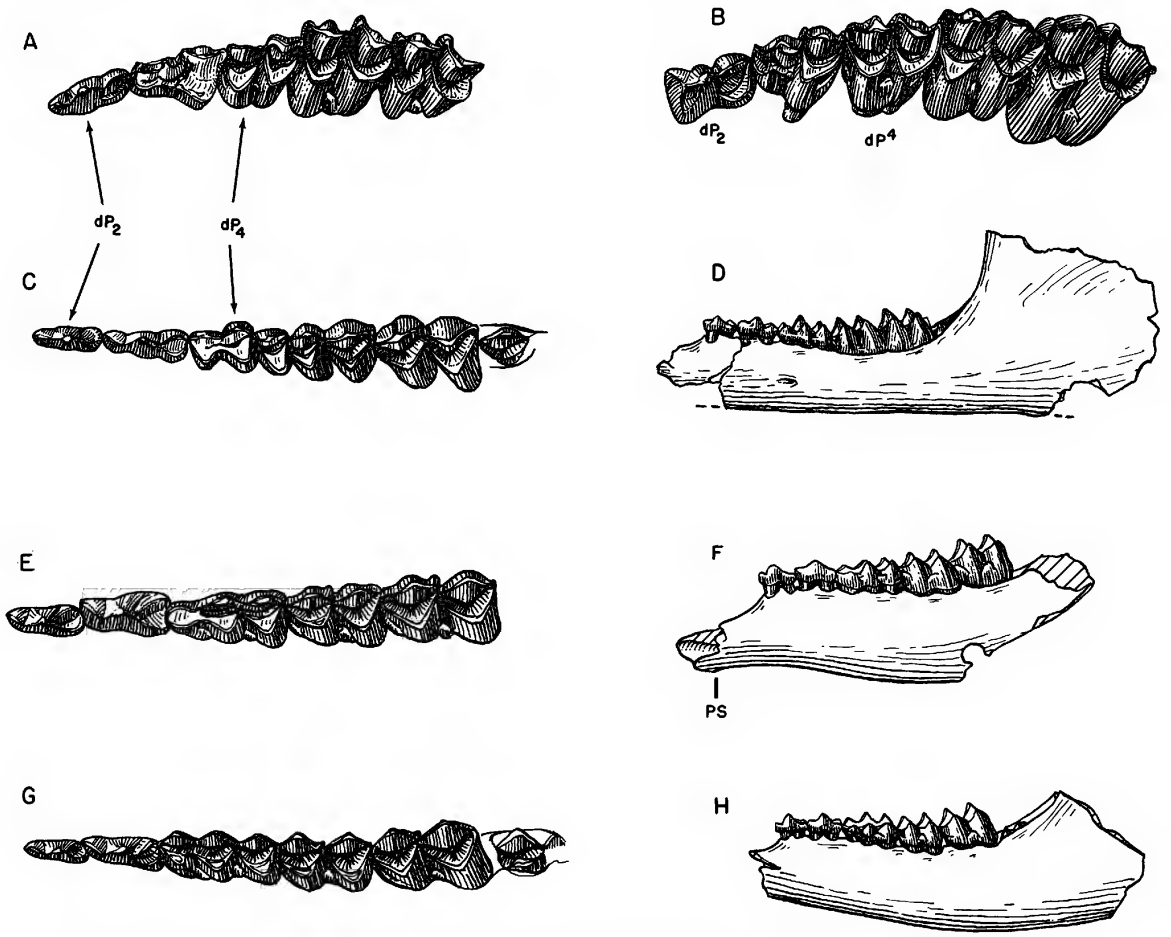

FIG. 5. A. *Leptomeryx evansi*, immature partial skull with dP^2-M^3 (unerupted), AMNH 39451, from the Scenic Member of the Brule Formation, South Dakota; dP^2-M^2, occlusal view. ×2. B. *Pseudoparablastomeryx scotti*, left immature maxilla with dP^2-M^2,9 F:AM 53394, from the type locality, Dawes Co., Nebraska, occlusal view. ×2. C, D. *Leptomeryx evansi*, AMNH 39452, right immature ramus with dP_2-M_3 (germ), from the Scenic Member of the Brule Formation, South Dakota; C. Occlusal view, reversed. ×2. D. Lateral view, reversed. ×1. E-H. *Pseudoparablastomeryx scotti* from early Barstovian deposits in Nebraska and Texas. E, F. F:AM 53400, right immature partial ramus with dP_2-M_2, from Sioux Co., Nebraska; E. Occlusal view, reversed. ×2. F. Lateral view, reversed. ×1. G, H. F:AM 95489, right immature partial ramus with dP_2-M_3 (germ) from San Jacinto Co., Texas; G. Occlusal view, reversed. ×2. H. Lateral view, reversed. ×1.

(germ) from Texas and two immature partial rami (F:AM 53400 and 53404) with dP_2-M_3 (broken) from Nebraska. In addition, dP_4 is present in two jaws from the type locality, Observation Quarry. Our description, however, is based for the most part on F:AM 95489, which shows little wear.

dP_2 (see fig. 5) is a small simple double-rooted tooth, which resembles the tooth that succeeds it. Basically, it consists of an anterior crest, a comparatively large primary cusp, and a relatively long posterior crest with a small but distinct crescent enclosing a small shallow fossettid. A minute anterolingual groove and a larger lingual groove behind the primary cusp are present. Compared with *Leptomeryx evansi*, dP_2 of *P. scotti* is smaller and less elongate with both the anterior and posterior crests relatively shorter.

dP_3 also strongly resembles P_3. The anterior crest is well developed and proportionally longer with a stronger anterolingual groove than that of dP_2. The primary cusp is larger and projects more lingually than that of dP_2. A prominent lingual groove separates the primary cusp from the posterior crescent. A posterior crescent emerges about midway of the long posterior crest to form a small fossettid. dP_3 is less elongate and less molariform than that of *Leptomeryx evansi.* In the latter, the talonid of dP_3 is longer, wider, and more molariform than that of *P. scotti*, with the posterior crest and crescent joining to resemble the lingual and buccal anteroconids of dP_4 that follows.

As in all artiodactyls, dP_4 is molariform with the three characteristic lobes. The anterior lobe is small with a well-developed cingulum-like buttress on the anterior of the buccal anteroconid. Unlike that on the molars, the buttress extends posteriorly around the buccal anteroconid and connects with the median pillar at the base of the crown between the buccal anteroconid and the protoconid. The last two lobes of dP_4 resemble those of M_1 but are smaller and lower crowned with smaller and shallower fossettids. The vertical ribs on the metaconid and entoconid are weak and less prominent than those of M_1. The metastylid is moderately strong and slightly larger than that of M_1 with a shallow groove separating it from the entoconid. dP_4 of *P. scotti* differs from that of *L. evansi* in the stronger buttress on the anteroconid, the weaker stylids, the much stronger cingulum pillars separating the buccal anteroconid, the protoconid, and the hypoconid, and the lower crowned metaconid.

Limbs. Definite association of limbs and dentition of *Pseudoparablastomeryx* is unknown. Frick (1937, p. 249) questionably referred unassociated limbs from the type locality to *P. scotti.* The tentative assignment of these limbs to *P. scotti* was no doubt influenced by the fact that both the dentition and the limbs represent the smallest known artiodactyl from that locality. Furthermore, the limbs, for the most part, resemble those of the Blastomerycinae but are shorter proportioned with some features in common with *Leptomeryx evansi.* This combination of features strengthens Frick's tentative assignment of these elements to *P. scotti.*

The distal end of the humerus (FBAM 33766A), which Frick (1937, p. 249) questionably referred to *P. scotti* is much smaller than that of *Pseudoblastomeryx advena* (Matthew, 1908) and near the size of the larger humeri included in the associated remains (AMNH 38910) of *Leptomeryx evansi* from South Dakota. The trochlea is less oblique to the upright shaft, and the articular surface of the mesial condyle in *P. scotti* is smaller relative to the lateral condyle than in *Blastomeryx elegans.* Furthermore, the coronoid fossa is shallower with the trochlear surface extending less deeply into the fossa than in *B. elegans.* In the above features the humerus resembles that of *L. evansi.* It differs from the latter, however, in a relatively larger lateral condyle and a deeper olecranon fossa. The humerus of *P. scotti* has a combination of derived features that are seen in the Blastomerycinae and primitive features in common with *L. evansi.*

Frick (1937, p. 249) questionably referred the proximal end of a radius (FBAM 33766) and doubtfully referred a right radius (FBAM 34027) to *P. scotti.* The proximal articular surface of each radius corresponds closely to the distal condyle of the above humerus, and we are referring both to *P. scotti.* The length of the radius (80.5 mm.) is only slightly greater than that (76.0 mm.) of an articulated limb (AMNH 38910) of *L. evansi.* Moreover, the limb ratio between the length of the radius (80.5 mm.) and the unassociated metacarpus (49.0 mm.) is similar to that (76.0 and 43.0 mm.) of the above articulated limb (AMNH 38910) of *L. evansi.* The relatively

short metacarpus in *P. scotti* is a plesiomorphic feature in common with *L. evansi* and is in sharp contrast to the derived condition in the Blastomerycinae in which the length of the metacarpus approximates that of the radius. For example, in the type (F:AM 31360) of *Parablastomeryx gregorii* the length of the metacarpus (151.0 mm.) slightly exceeds that of the radius (149.0 mm.). A marked rugosity on the posterior surface of the radius indicates that the ulna was loosely attached to the radius for its full length as in both *L. evansi* and *P. gregorii.* The proximolateral articular surface of the radius in *P. scotti*, which articulates with the lateral condyle of the humerus, is larger relative to the proximomesial surface than in the Blastomerycinae. This corresponds to our observation of the humerus in which the mesial condyle is also relatively smaller. In comparison with *L. evansi* the proximal facets of the radius, which articulate with the condyles of the humerus, are separated by a deeper groove with a deeper notched posterior border to coincide with the more prominent lateral condylar ridge of the humerus. The distal end of the radius consists of two main facets for the scaphoid and lunar plus a reduced articular surface which appears to combine with a small facet on the distal end of the ulna to form the articular surface for the cuneiform. Anteriorly, the scaphoid facet is wide and deeply concave; it narrows posteriorly and projects distally. A sharp ridge separates the lunar from the scaphoid articular surface. The lunar facet is less concave but narrower posteriorly than that for the scaphoid. In contrast to *L. evansi* the distal facets for the scaphoid and lunar in *P. scotti* are relatively smaller, narrower, and more concave. Moreover, the articular surface for the cuneiform is missing entirely in *L. evansi* with the cuneiform contacting only the distal end of the ulna. The morphology of the distal end of the radius closely resembles the derived condition in the Blastomerycinae. This is, no doubt, an example of convergence and can be explained as a necessary step in adapting to the fused metacarpals III and IV.

One unassociated metacarpus (FBAM 33765) is referred to *P. scotti.* The length of the metacarpus is 49.0 mm. and it is robust and solidly fused. Based upon the length of these unassociated limbs, the short metacarpus-radius proportion in *P. scotti* is similar to that of *L. evansi* and unlike that of the *P. gregorii* in which these two limbs are of about equal length. Metacarpals III and IV are solidly fused and without the prominent groove along the line of fusion that is sometimes seen in artiodactyls. A rudimentary metacarpal II is indicated by what appears to be a vestigial remnant that is fully coossified to the proximomesial surface of the metacarpus. The proximolateral surface of the metacarpus is broken, thus precluding the recognition of either the presence or absence of metacarpal V. The lack of a marked depression or rugosity over most of the posteromedial part of the metacarpus suggests that the lateral metacarpals were incomplete. This is unlike the metacarpus (AMNH 13015) of *P.* (*Pseudoblastomeryx*) *advena* (Matthew, 1907) in which a depression for the entire length of the metacarpus indicates the presence of full length lateral metacarpals II and V. In the metacarpus of *P. scotti* a distolateral and a distomesial flattened surface extend upward for about 10.0 mm. above the trochlea to indicate the presence of distal remnants of metacarpals II and V. The keel on the distal end of the metacarpus is strong and continues onto the anterior surface of the trochlea, whereas in *L. evansi* the keel is confined to the posterior surface and disappears completely on the distal end before reaching the anterior surface of the trochlea. The fused metacarpals III and IV, the reduction of metacarpals II and V, and the strong distal keel in *P. scotti* are derived features that are also present in the Blastomerycinae.

Frick also questionably referred a metatarsus (FBAM 33764) from the type locality to *P. scotti* and questioned the identity of a somewhat longer metatarsus (FBAM 34027A). We are referring both of these specimens along with additional metatarsi to *P. scotti.* The metatarsus is solidly fused, but unlike the metacarpus, the line of fusion on the anterior surface is marked by a prominent groove. A strong keel encircles the distal trochlea of the metatarsus. The metatarsi range in length from 66.0 mm. (FBAM 33764) to 76.5 mm. (F:AM 95491). Based on unassociated metapodials the metatarsal length may be about one-third greater than the metacarpal length. If this is correct, the metatarsus is relatively longer than in the Blastomerycinae

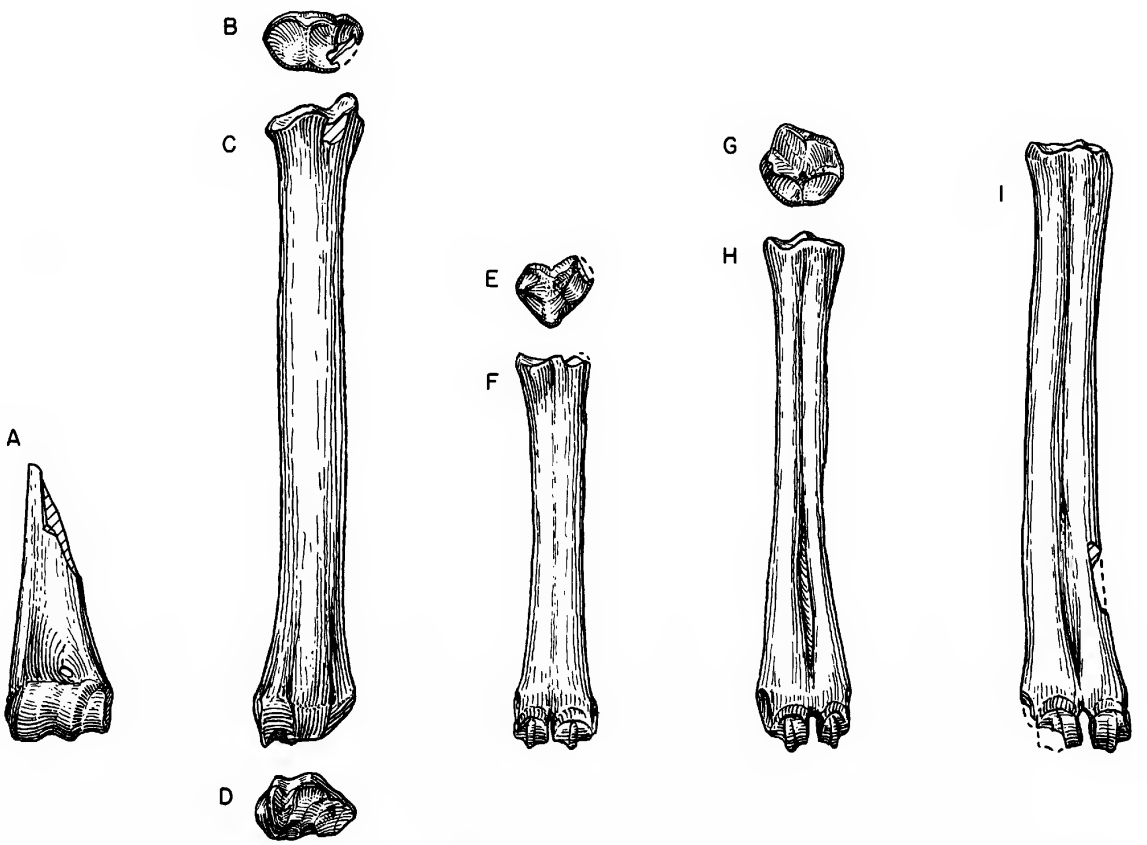

FIG. 6. *Pseudoparablastomeryx scotti*, limbs from Dawes Co., Nebraska; A. Left partial humerus, FBAM 33766A, anterior view. B-D. Right radius, FBAM 34027. B. Proximal view, reversed. C. Anterior view, reversed. D. Distal view, reversed. E, F. Right metacarpus, FBAM 33765. E. Proximal view, reversed. F. Anterior view, reversed. G, H. Left metatarsus, FBAM 33764. G. Proximal view. H. Anterior view. I. Left metatarsus, F:AM 95491, anterior view. All ×1.

with its metatarsus averaging from 15 to 18 percent longer than the metacarpus. Frick (1937, p. 249) likewise pointed out that the metatarsus (FBAM 34027A) is somewhat longer proportioned than the other limbs assigned to *P. scotti*. A proportionally longer metatarsus is a plesiomorphic feature in common with *L. evansi*.

Pseudoparablastomeryx francescita (Frick)
Figure 7; table 3

Blastomeryx francescita Frick, 1937, p. 242, fig. 23.

Type. F:AM 31425, right partial ramus with M_1 (broken)-M_3 from the Pojoaque Member (Valentinian) of the Tesuque Formation, Santa Cruz area, Santa Fe County, New Mexico.

Known Distribution. Valentinian of New Mexico.

Referred Material. From the Pojoaque Member of the Tesuque Formation, Santa Fe County, New Mexico: F:AM 31397, right partial ramus with P_3 (root) and P_4 (broken)-M_2 (broken), Santa Cruz; F:AM 53405, left ramus with diastema and broken symphysis showing the base of the alveoli of the incisors and P_2 (alveolus)-M_3, Pojoaque Bluffs; F:AM 53406, left ramal fragment with diastema P_2-P_3 alveoli and roots, Pojoaque Bluffs; and F:AM 53407, right partial ramus with incomplete diastema and P_2 (alveolus)-P_4, Pojoaque Bluffs.

Revised Diagnosis. Differs from *P. scotti* in that the molars average smaller (tables 2 and 3); P_3 and P_4 larger relative to the size of the molars,

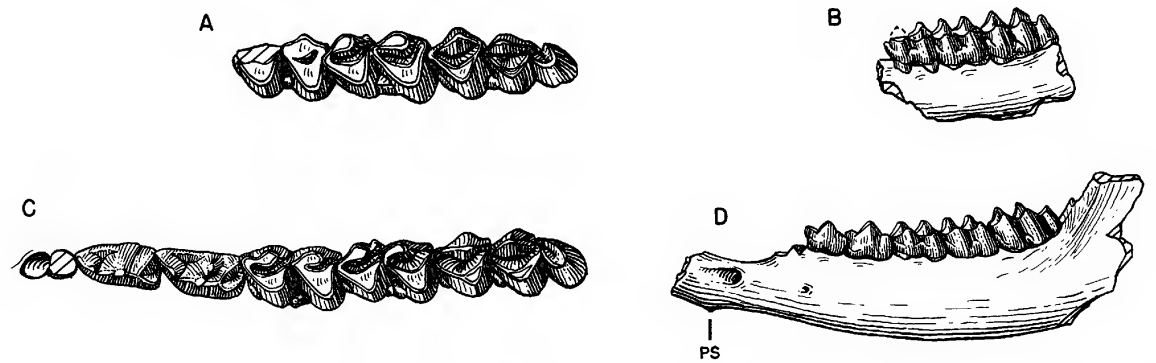

FIG. 7. *Pseudoparablastomeryx francescita*, mandibular rami from Santa Fe Co., New Mexico; A, B. Type. F:AM 31425. A. Occlusal view, reversed. X2. B. Lateral view, reversed. X1. C-D. F:AM 53405. C. Occlusal view. X2. D. Lateral view. X1.

TABLE 3
Measurements (in Millimeters) of the Lower Dentition of *Pseudoparablastomeryx francescita* (Frick)

		F:AM No.[a] 31425	F:AM No. 31397	F:AM No. 53405	F:AM No. 53407
P_3	Length	–	–	5.5	6.0
	Width	–	–	2.8	3.1
P_4	Length	–	(6.0)[b]	6.0	6.5
	Width	–	–	3.0	3.5
M_1	Length	(6.0)	5.9	6.1	–
	Width	–	3.6	4.0	–
M_2	Length	6.5	(7.0+)	6.4	–
	Width	4.3	–	4.3	–
M_3	Length	9.0	–	8.5	–
	Width	3.9	–	4.1	–

[a]F:AM no. 31425 is the type of *P. francescita* (Frick).
[b]Measurements enclosed in parentheses are approximate.

which are noticeably narrower and taller crowned.

Discussion. Frick (1937, p. 242) described *Blastomeryx francescita* based upon a fragmentary jaw. The type (F:AM 31425) is a ramal fragment with only the molars, and Frick referred two more fragmentary jaws of which one (F:AM 31434) is believed referable to *Blastomeryx*. Since 1937, three additional specimens have been found that are referable to this taxon, and one, an almost complete mandibular ramus (F:AM 53405) shows the postsymphysial diastema and the premolar area. P_2 is represented by an alveolus but P_3 and P_4 are present and proportionally larger than in *Blastomeryx*. P_3 and P_4 are also less complex with a more reduced metaconid. The most diagnostic feature of the ramus is the extremely abbreviated diastema. The distance from the postsymphysis to P_2 is much less than that of *Blastomeryx* and comparable with that of the type of *Pseudoparablastomeryx scotti*. In the referred ramus (F:AM 53405) M_3 length (8.5 mm.) is 1.2 times greater than the postsymphysial-P_2 length (7.0 mm.). This extremely short diastema is unlike any member of the Blastomerycinae but comparable with *Pseudoparablastomeryx* and characteristic of the Leptomerycinae.

RELATIONSHIPS

The phylogenetic position of *Leptomeryx* and its allies was problematical almost from the beginning. The essential question of whether they were cameloid or cervoid received contradictory answers for nearly a century. In his early description of *Leptomeryx* Leidy (1853, p. 394; 1869, p. 165) noted many cervoid and traguloid features. Then Rütimeyer (1883, p. 98), the great Swiss student of deer and other ruminants, severely criticized Leidy's views and stated authoritatively that the features of the mandible

and the premolars bespoke close relationships with the abundant North American camels and oreodonts. In his earliest study of *Leptomeryx* Scott (1891, p. 376) recognized traguloid features, but in his most important later contributions, beginning in 1899 and continuing to 1940, he elaborated and defended Rütimeyer's opinion.

Meanwhile, Matthew had begun to espouse the cervoid point of view. In 1908 he advocated the cervoid affinities of *Leptomeryx*. He stated (*op. cit.*, p. 555): "Its occurrence in the American Oligocene, contemporaneous with much more advanced Pecora of the Old World, precludes regarding it as genetically ancestral to the Cervidae as a whole. It may be ancestral through *Blastomeryx*, however, to the American deer."

Later, however, Matthew retreated from this view, noting (1926, p. 7) that *Blastomeryx* and its near allies "appear suddenly . . . an invading group, not derived from autochthonic predecessors." Although Matthew did not explain this change in his thinking, it surely sprang from his vastly increased knowledge of ruminant evolution, in particular from his own important studies of early Tertiary taxa from Mongolia. Thus, he specifically remarked (1926, p. 8) that the ancestry of such traguloids as *Leptomeryx* and *Hypertragulus* lay close to *Archaeomeryx*.

Even this final, widely accepted view of Matthew's has been confused to a degree, for in a posthumous paper (Matthew, 1934), the exact relationship between Tragulidae and Cervidae was presented in a very generalized way, with *Leptomeryx* and the European *Prodremotherium* placed in a line of ascent just below *Blastomeryx* and the European *Dremotherium*. Presumably this is the basis for Frick's and Scott's later statements that Matthew still considered "*Leptomeryx* ancestral to certain deer." (Frick, 1937, p. 620).

The present study raises two fundamental questions regarding the phylogenetic relationships of the Leptomerycidae. First, what are the relationships of the early members to the Hypertragulidae? And second, what are the relationships of the later Leptomerycinae to the Blastomerycinae?

The Leptomerycidae may be separated from the Hypertragulidae on the basis of a number of synapomorphous (shared derived) characters as defined by Hennig (1966). Morphological features of the Leptomerycidae that are derived with respect to the Hypertragulidae are: (1) a vestigial upper canine,[1] (2) a well-developed protocone on the second and third upper premolars, (3) an enlargement of the lingual cuspids on the third and fourth lower premolars, and (4) a large procumbent tusklike I_1. Of the above characters, the large procumbent tusklike I_1 is believed to be a unique derived character for the Leptomerycidae. A comparison of important characters between the contemporaneous *Leptomeryx* and *Hypertragulus* is summarized in table 4.

The second question concerns the possible relationship between the later Leptomerycinae and the Blastomerycinae. We have noted above the long history of debate over whether the Blastomerycinae were immigrants to North America or were descendants of Leptomerycinae. And our transfer of *Pseudoparablastomeryx scotti* from the Blastomerycinae, where Frick had assigned it, to the Leptomerycinae reopens that debate.

A review of the problem in the light of more complete material than was available to previous students convinces us that no close phylogenetic relationship exists between the Leptomerycinae and the Blastomerycinae. Our study supports the view stated by Matthew in 1926 that the Blastomerycinae appear suddenly as an invading group from the Old World. The Leptomerycinae have a number of derived features not shared with the Blastomerycinae, including the reduced upper canine, the procumbent lower incisors, the enlarged tusklike I_1, and a distinctly separated first lower premolar. The first two of these features have already been noted in comparisons with the Hypertragulidae, but they are also derived with respect to the Blastomerycinae. The distinction of the lower first premolar requires further explanation.

In *Leptomeryx* a small caniniform P_1 stands in

[1]Although the upper canine in *Nanotragulus* is reduced in size, as seen in the type of *N. intermedius* Schlaikjer (1935, p. 178), the root is long and the canine is functional and occludes with P_1. The upper canine of *Nanotragulus* is much smaller than in *Hypertragulus*, but is not vestigial as in *Leptomeryx*.

TABLE 4
Morphological Comparisons of *Hypertragulus* and *Leptomeryx*

	Hypertragulus	*Leptomeryx*
Cranial Features		
Postorbital bar	Incomplete	Complete
Postparietal foramen	Small or absent	Large
Mastoid foramen	Small, posterior	Large fissure-like, anterior
Auditory bulla	Small	Moderate
Dental Features		
Upper canine	Enlarged	Vestigial
First upper premolar	Two-rooted	Lost
P^2 and P^3	Protocones small to absent	Protocones large
First lower premolar	Enlarged	Small
First lower incisor	Normal	Tusklike
Lower incisors	Oblique	Procumbent
Postcranial Features		
Ulna and radius	Ulna relatively light and fully fused with radius	Ulna moderately heavy and unfused with radius
Trapezoid and magnum	Separate	Coalesced
Cuneiform facet of radius	Present	Missing
Metacarpal I	Reduced	Lost
Distal vestige of fibula	Fused with tibia	Separate from tibia
Metatarsals III and IV	Unfused	Fused
Metatarsals II and V	Slender and extend for almost the full length of metatarsals III and IV	Reduced to proximal remnants

the diastema midway between the incisiform series and the premolariform series. Scott (1940, p. 539) is surely correct in supposing that within the ancestry of the Leptomerycinae this tooth must have had a canine-like function as in *Hypertragulus*. In the Blastomerycinae, on the other hand, the first lower premolar had a very different history. A small root or alveolus in a few specimens, including the type (AMNH 13224) *P. (Problastomeryx) olcotti* (Matthew, 1908) and the type (AMNH 13822) of *P. (Problastomeryx) primus* (Matthew, 1908), indicated the position of P_1 anterior to P_2. The position is similar to that of the first premolar in such Gelocidae as *Gelocus* and *Prodremotherium* (Webb and Taylor, MS) which lie near the presumed Old World ancestry of the Blastomerycinae. It is presumably the plesiomorphous (primitive) condition for ruminants in general. Thus the condition of the first lower premolar to Leptomerycinae is a derived character with respect to its condition in the Blastomerycinae. Late members of both subfamilies lost this premolar altogether and thus developed a superficial parallel resemblance.

It is astonishing to note the number of progressive features in which the latest members of the Leptomerycinae parallel the contemporaneous Blastomerycinae. (See table 5). Such features of *Pseudoparablastomeryx* as the short broad skull, the elaborate upper and lower premolars, the loss of $P\frac{1}{1}$, the anterobuccal buttress in the lower molars, the fused metacarpals, and complete distal keels on the metapodials, are shared with the Blastomerycinae. These progressive features in common do not alter the force of the derived features cited above which indicate that it is impossible for the Blastomerycinae to be derived from the Leptomerycinae. We have shown above that the loss of P_1 was accomplished by wholly different means in these two subfamilies, and it is possible that these other features are also parallel developments. For example, the fusion of metacarpals III and IV

TABLE 5
Morphological Comparisons of *Pseudoparablastomeryx* with *Leptomeryx* and the Blastomerycinae

Features	In common with *Leptomeryx* but not with the Blastomerycinae	In common with the Blastomerycinae but not with *Leptomeryx*
1. Short broad skull shape	–	X
2. Vestigial upper canine	X	–
3. Short postcanine diastema	X	–
4. Elongate symphysis	X	–
5. Procumbent incisors	X	–
6. I_1 relatively large, procumbent, and tusklike with tall crown and elongate root	X	–
7. Procumbent lower canine	X	–
8. Loss of P_1	–	X
9. Development of anterobuccal buttress on molars	–	X
10. Metacarpals III and IV fused	–	X
11. Completion of the distal keel on the metapodials	–	X
12. Distal end of radius with articular facet for the cuneiform	–	X

was probably a parallel development which in turn produced other parallel resemblances such as the completion of the distal keels and the modified radial articulation described, page 16. They probably show instead that both groups were responding in similar ways to similar environmental pressures. It is not surprising that two generations of paleontologists repeatedly tried to unite these two separate subfamilies. Phylogenetic systematics must be alert to the perils of such parallel evolution.

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